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## A New Fossil Species of Termite from Mexican Amber, *Mastotermes electromexicus* (Isoptera, Mastotermitidae)

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### ABSTRACT

A new fossil species of termite, *Mastotermes electromexicus*, is described from upper Oligocene–lower Miocene amber of Chiapas, Mexico. This is the first amber fossil of the family Mas-

totermiidae, the first fossil soldier of any termite species, and the first species of *Mastotermes* from the New World to be reported.

### INTRODUCTION

The purpose of the present paper is to describe a new species of *Mastotermes* from fossil specimens preserved in amber from Chiapas, Mexico. All termite fossils hitherto reported belong to the reproductive caste, and all descriptions of them have been based on fragments, usually partial or whole wings only. The description of this new species is based on a remarkable series of specimens from the Museum of Paleontology, University of California, Berkeley, which includes fragments of an alate, the partial head of a soldier, and about 17 full and partial specimens of nymphs (larvae) in different stages of development. This is the first soldier ever reported in the fossil record of termites and the first fossil sampling to represent all castes—imago, sol-

dier, and worker—as well as the first to represent young larvae in different stages of development. It is also the first reported amber fossil of *Mastotermes* or of any other genus of the Mastotermitidae, all others (the wing fragments) being shale fossils. Since the specimens are in different pieces of amber which were not collected in precisely the same location, it would be hazardous to label this a “first fossil termite colony,” though one is tempted to do so.

It is recognized that the family Mastotermitidae is, in several morphological characteristics, the most primitive family of the order Isoptera, closest to the order Blattodea and to the blattoid-like ancestor from which termites and roaches evolved (Emerson, 1965;

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Krishna, 1970; Emerson and Krishna, 1975). (Among the living Blattodea, *Cryptocercus punctulatus* Scudder, the subsocial, wingless, wood-eating roach, bears a close relationship to *Mastotermes darwiniensis* Froggatt [McKittrick, 1964, 1965; Krishna, 1970].)

The most recent review of the family Mastotermitidae was done by Emerson (1965), who included in it the two fossil genera *Spargotermes*, from the Oligocene–Miocene of South America, and *Blattotermes*, from the Eocene of the United States and Australia; the fossil and living genus *Mastotermes*, from the Oligocene to Miocene of Europe and Recent Australia; and one fossil genus of doubtful validity, *Miotermes*.

The family Mastotermitidae is represented today by only one relict living species, *Mastotermes darwiniensis*, and is restricted to northern Australia. The fossil record of the family in the Tertiary shows that it once had a much wider distribution: South America, Europe, and Australia. Even though no Mesozoic fossil exists, this widespread geographical distribution, along with the derived characters shared with the ancient Blattodea, strongly suggests that the family probably existed in the Late Permian or Early Mesozoic (Triassic), before the breakup of Pangaea (Emerson, 1955, 1965; Emerson and Krishna, 1975).

Until now, the genus *Mastotermes* has been represented by six fossil species—*Mastotermes anglicus* von Rosen, from the middle Oligocene of the Isle of Wight, England; *M. bournemouthisensis* von Rosen, from the upper Eocene of Hampshire, England; *M. croaticus* von Rosen, from the lower Miocene of Radoboj, Croatia, Yugoslavia; *M. haidingeri* (Heer), from the lower Miocene of Radoboj, Croatia, Yugoslavia; *M. heeri* (Goeppert), from the upper Oligocene of Schlesien, Germany; and *M. minor* Pongrácz, from the lower Miocene of Radoboj, Croatia, Yugoslavia—and one living species, *M. darwiniensis* Froggatt from northern Australia. The new fossil species described here, *M. electromexicus*, from the upper Oligocene to lower Miocene of Chiapas, Mexico, will be the first representative of this genus from the New World. This new fossil species is remarkably close in its morphology to the living species *M. darwiniensis* from Australia.

The climate of Chiapas, Mexico, at the time of the fossilization of *Mastotermes electromexicus* was, as it is at present, tropical (Emerson, 1965, 1967, 1969, 1971; Hurd, Smith, and Durham, 1962; Langenheim, 1969). The fact that the living species *M. darwiniensis* is also tropical (found in the portion of Australia north of the Tropic of Capricorn) suggests that the genus *Mastotermes* and also probably the entire family Mastotermitidae are tropical, with some species having invaded warm-temperate climates, since the fossils from Europe and North America are from the Eocene through the Miocene, when the climate in these places was warmer than it is today (Emerson, 1965, 1971; Chandler, 1964).

#### ACKNOWLEDGMENTS

We are indebted to the late Mr. Joseph H. Peck, of the Museum of Paleontology, University of California, Berkeley, who made this fossil material available to us for study; to Ms. Bonnie Burns, Department of Invertebrates, American Museum of Natural History, for preparing and polishing some of the amber pieces; and to Dr. Valerie Krishna for editorial assistance.

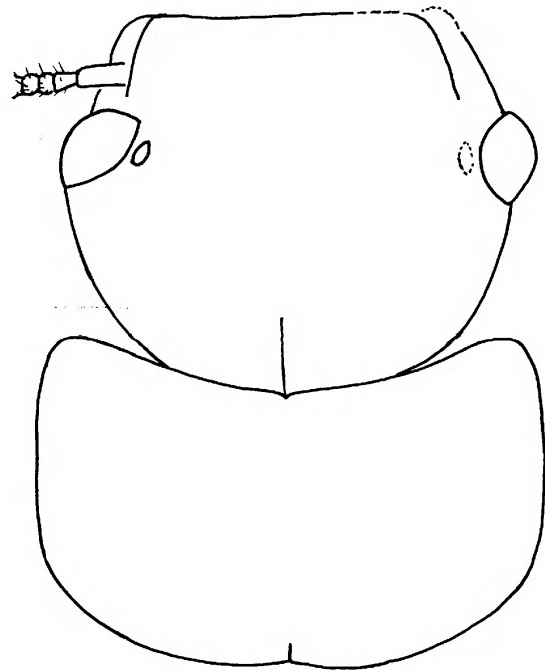
#### *Mastotermes electromexicus*, new species

IMAGO (FIG. 1): Pilosity obscure. Head surface rough and slightly depressed (as in *darwiniensis*); rounded ridge above base of antenna. Y-suture not visible. Eyes ovalish, not touching antennal fossa; front margin slightly rounded; in dorsal view moderately convex, extending beyond side margins of head capsule. Ocellus not touching eye; distance from eye a little less than its own width (touching eye in *darwiniensis*). Postclypeus shorter than its width, front margin straight (as in *darwiniensis*). Antenna moniliform, probably complete, with 28 articles; second longer than third; third, fourth, and fifth very short and about equal. Pronotum as wide as, or wider, than head, flatly arched, with sides convex (as in *darwiniensis*), front margin widely concave, with no indentation in middle, posterior margin broadly emarginate. Impression of fragment of hind wing base on surface of amber eroded, making veins difficult to dis-

TABLE 1  
Measurements (in Millimeters) of Imagoes of  
*Mastotermes electromexicus*, New Species, and  
*Mastotermes darwiniensis* Froggatt

	<i>electro- mexicus</i> (para- type)	<i>darwin- iensis</i>
Width of head with eyes	4.15	3.30–3.35
Length of eye	0.80	0.95–1.00
Width of eye	0.66	0.89
Eye from base of antennal fossa	0.07	touching
Ocellus from eye	0.10	touching
Length of ocellus	0.25	0.30–0.40
Width of ocellus	0.15	0.22–0.25
Length of first antennal article	0.37	0.32
Length of second antennal article	0.24	0.18
Length of third antennal article	0.12	0.08
Median length of postclypeus	0.30	0.28
Maximum length of pronotum	2.50	2.50–2.65

tinguish (see fig. 2). Subcosta with superior branches, arising from  $R_1$ ;  $R_1$  branched,  $R_{2+3}$  arising separately from wing scale and not branched from  $R_s$  (in *darwiniensis* branched from  $R_s$  some distance away from scale).  $R_s$  branched from median near scale, inferior branches of CuA not visible; CuP not clear,  $A_1$  with three or more inferior branches, but other branches not visible. Anal fold visible. Anal lobe with about six veins visible. Mem-



2.0 mm.

FIG. 1. Head and pronotum of paramorphotype imago of *Mastotermes electromexicus*, new species, from locality B-7044-24, Chiapas, Mexico.

brane reticulations (archidityon) not clearly visible, but a section of another wing seen through amber shows a small part with archidityon.

TABLE 2  
Measurements (in Millimeters) of Soldiers of *Mastotermes electromexicus*, New Species, and  
*Mastotermes darwiniensis* Froggatt

	<i>electromexicus</i> (holotype)	<i>darwiniensis</i>
Width of head below antennal fossa	3.60	2.80–2.90
Left mandible		
Length from tip to rear edge of condyle	2.26	1.86–2.00
Length from tip to notch on outer margin	1.74	1.16
Length from apical tip to tip of first marginal tooth	0.65	0.55–0.65
Width from tip of first marginal tooth to outer margin	0.60	0.48
Width of apical tooth (blade) from basal inner margin to outer margin	0.43	0.32
Width of anteclypeus	0.75 (approx.)	0.93
Median length of anteclypeus	0.46	0.30–0.35
Width of labrum	0.95	0.85
Median length of labrum	0.65	0.60–0.65



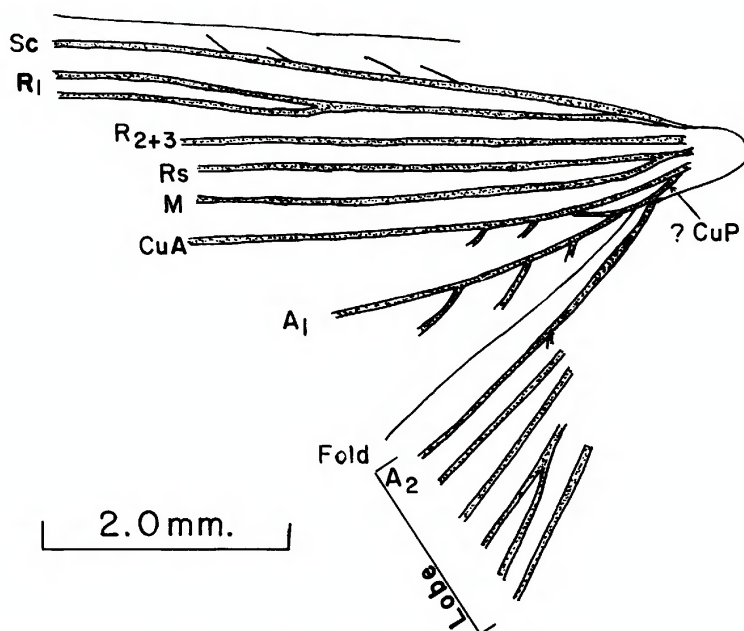


FIG. 2. Basal portion of hind wing of *Mastotermes electromexicus*, new species, from locality B-7044-24, Chiapas, Mexico. Abbreviations: A<sub>1</sub>, first anal; A<sub>2</sub>, second anal; CuA, anterior cubitus; CuP, posterior cubitus; Lobe, anal lobe; M, media; R<sub>1</sub>, first radius; R<sub>2+3</sub>, joined second and third radius; Rs, radial sector; Sc, subcosta.

SOLDIER (FIG. 3) (description based on a fragment of front of head and of a left mandible): Head with a long hair on each side in front, below antennal fossa; antennal segments with long hairs on tip and on sides, longest bristle 0.20 mm. (0.14 mm. in *darwiniensis*); labrum with four long hairs near tip, 0.32 mm. in length (0.41 mm. in *darwiniensis*) and a few much shorter hairs on sides. Head anteriorly wider, with sides converging less strongly toward base of mandibles than in *darwiniensis*; strongly concave rounded depression below antennal fossa and sharp projecting ridge above it, at top rear edge (as in *darwiniensis*). Anteclypeus longer than half its width, middle line present, side margins moderately concave. Labrum short, arched in middle; wider than long, sides strongly rounded, including junction with anteclypeus; anterior margin somewhat distorted, appearing straight to flatly rounded (as in *darwiniensis*). Left mandible with outer margin evenly curved from basal notch toward tip of apical tooth, gradually curving inward apically, but not hooked (more sharp-

ly curved in *darwiniensis*); inner margin of apical tooth curved gently from tip to junction with first marginal tooth; first marginal tooth large and triangular, angle of junction of first marginal tooth with base of inner margin of apical tooth not very sharp, but curved and blunt, wider than a right angle, front margin a little shorter than posterior margin; outer basal margin of mandible behind notch flatly convex (flatly concave in *darwiniensis*). Antenna broken, with 11 articles present; first three times the length of second, second slightly more than twice the length of third, third shortest, fourth to seventh slightly longer than third, eleventh nearly twice the length of third.

NYMPHS (LARVAE) (FIG. 4) (description based on fragments of several nymphs without wing pads [larvae], belonging to different instars, in 13 different pieces of amber): Head and pronotum with many bristles, longest 0.17 mm.; legs with numerous long hairs, bristles, and several short spines. Small eye spot visible. Labrum with sides and front curved (similar to *darwiniensis*; see fig. 31,

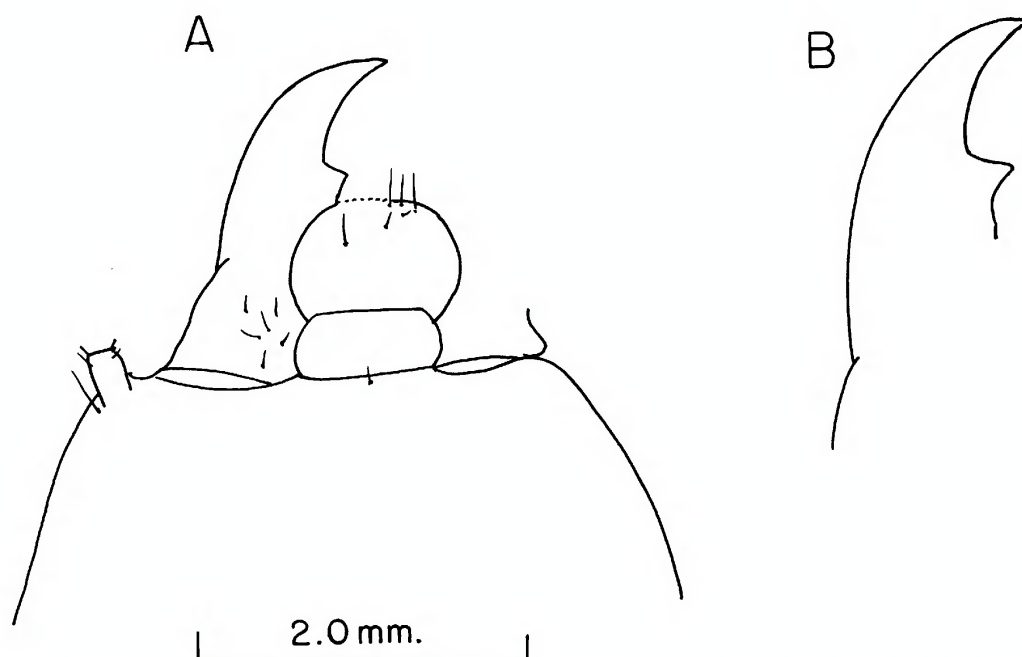


FIG. 3. Holotype soldier of *Mastotermes electromexicus*, new species, from locality B-5341-17, Chiapas, Mexico. A. Partial head capsule and left mandible. B. Left mandible. (Scale refers to A only.)

pl. xxii, Silvestri, 1909). Antenna with 24 articles (longer than in *darwiniensis*), first article longest, second longer than third, third slightly shorter than, or almost equal to, fourth. Pronotum, as in *darwiniensis*, saddle-shaped, with a line in middle and long, large

frontal lobe; front margin convexly rounded with a broad, shallow, but distinct median indentation, laterally front angles projected; sides angularly narrowing posteriorly, margins straight or slightly concave in middle. Prothoracic coxa with projecting ridge with

TABLE 3  
Measurements (in Millimeters) of Nymphs of *Mastotermes electromexicus*, New Species, and *Mastotermes darwiniensis* Froggatt

	<i>electromexicus</i>							<i>darwiniensis</i>
	B-8416-3	B-8414-6	B-7049-6	B-8413-126	B-5341-18	B-7044-25	B-7049-7	
Width of head	3.00	—	3.50	3.54	2.56	2.90	2.81	2.86–2.99
Length of labrum	0.75	0.61	—	—	—	—	0.61	—
Width of labrum	—	0.85	—	—	—	—	—	0.60
Length of postclypeus	0.50	0.30	—	—	—	—	0.36	0.30
Width of postclypeus	1.85	—	—	—	—	—	—	—
Median length of pronotum	1.95	—	1.75	—	1.71	—	—	1.39–1.48
Width of pronotum	—	—	2.75	—	—	—	—	2.20
Length of fore tibia	—	1.32	—	1.95	—	—	—	1.56
Length of middle tibia	—	1.34	1.80	2.08	—	—	—	1.71
Length of hind tibia	1.83	—	—	2.61	2.56	—	—	2.25
Length of cercus	—	—	—	0.46	0.52	—	—	0.43–0.44
Length of stylus	—	—	—	0.35	—	—	—	0.25–0.35

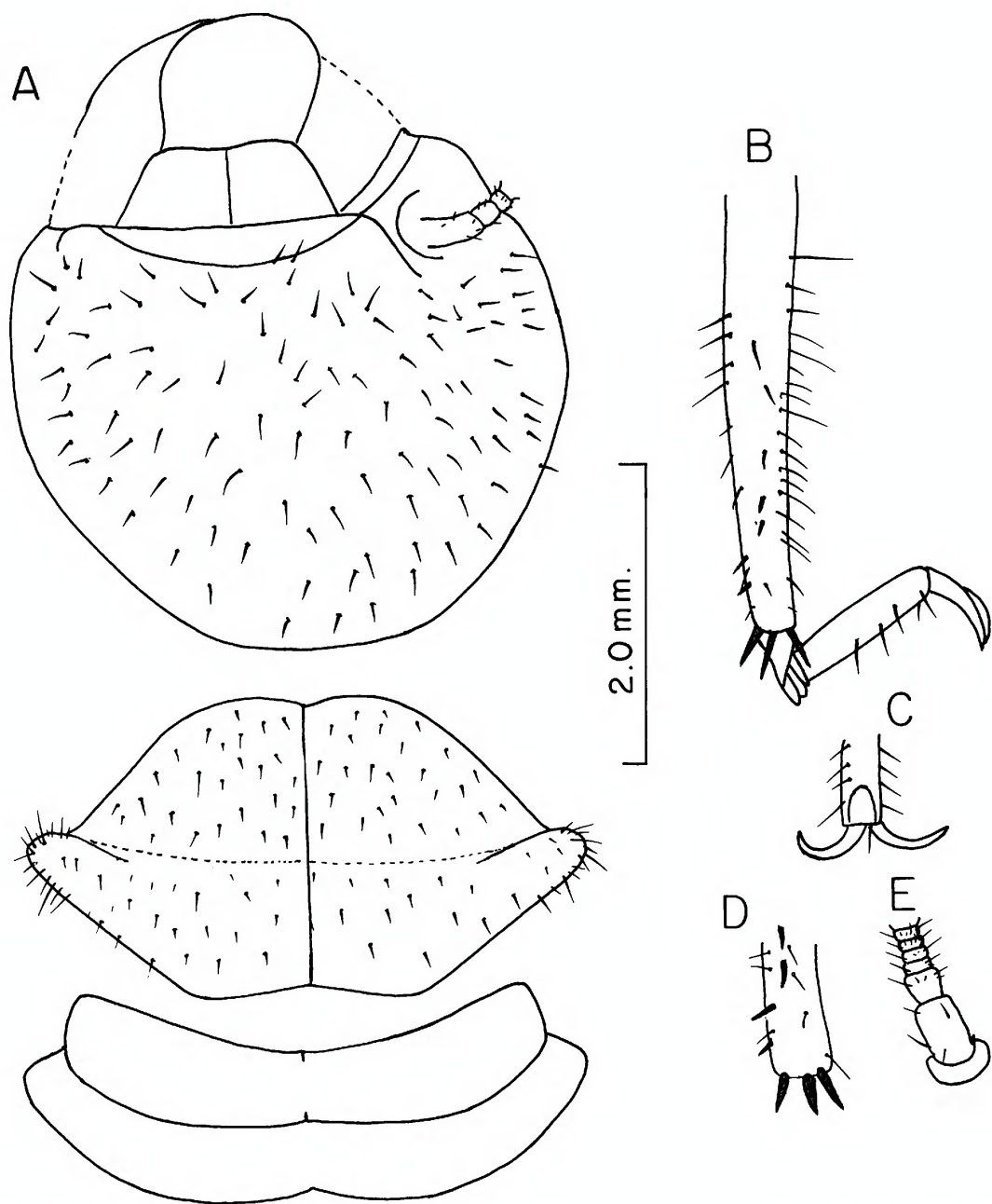


FIG. 4. Paratype nymph of *Mastotermes electromexicus*, new species. A. Head and pronotum from locality B-8416-3. B. Leg: tibia and tarsus, from locality B-7045-59. C. Basal portion of last tarsal segment with claws, from locality B-7045-59. D. Basal portion of tibia showing tibial spurs and spines, from locality B-7045-59. E. Basal portion of antenna, from locality B-7049-8. (Scale refers to A, B, and C only.)

spiny protrusions (similar to *darwiniensis*; see fig. 34, pl. xvii, Silvestri, 1909). Fore and middle femora and tibia each with a longi-

tudinal groove and two rows of short spines (15–16) along edges of groove; middle tibia with two or more short lateral spines on in-

side above spurs, as in *darwiniensis* (fig. 4D), a few additional spines above and outer to lateral spines. Tibial spurs 3:4:4; fourth spur on middle and hind tibia not clearly visible; spurs rough, probably with papillae, as in *darwiniensis*. Tarsus with five articles. Cercus with five articles, length about 0.46 mm. (0.43 mm. in *darwiniensis*); stylus long, about 0.35 mm. (0.29 mm. in *darwiniensis*).

COMPARISONS: The fossil *Mastotermes electromexicus*, new species, is astonishingly close in many respects to the living species *M. darwiniensis* Froggatt, but differs from it in the following respects. The soldier of *M. electromexicus* is larger; its head is wider anteriorly below the antennal fossa; the left mandible is longer and more robust; the outer margin of the left apical tooth is less sharply curved; the junction between the apical tooth and the first marginal tooth is curved rather than angular; the anteclypeus is longer; and the sides of the labrum are more rounded. The imago of *M. electromexicus* has a wider head and smaller eyes; the ocellus is smaller and not touching the eye; in the hind wing the first radius vein ( $R_1$ ) branching is closer to the base of the wing, and the fused second and third radius ( $R_{2+3}$ ) arises separately from the wing scale rather than from the radial sector (Rs); and the antenna probably has fewer articles.

SPECIMENS AND LOCALITIES: All the localities listed here are from the Simojovel Region, Chiapas, Mexico. The age of the amber-bearing formation (La Quinta) from these localities is assigned as upper Oligocene or Lower Miocene, age 26 million years or slightly older (Langenheim, 1969; Frost and Langenheim, 1974). Soldier (holotype), fragment of head with left mandible only, in a small piece of amber, which is hollowed out on one side, from locality B-5341-17,<sup>3</sup> village at San Pedro, 5 km. north of Simojovel, from right bank of Rio Pedro across from old church of San Pedro (lat. 17°1'N, long. 92°2'W) (type locality), acc. no. 1839.<sup>3</sup> Imago (paramorphotype), portion of head, thorax, and hind wing in a piece of amber 22 mm. long, 7 mm. wide, 9 mm. thick, and nymph

(paratype), head, thorax with legs, and part of abdomen in a separate piece of amber, both from locality B-7044-24, between Quechala and Tecpatan, right bank of Grijalva River, between lower end of big canyon and junction with the La Vena River. Nearly whole nymph and fragments of head of another nymph (paratypes) from locality B-5341-18, same locality data as holotype specimen. Nymph fragments (paratype), head, thorax, and abdomen from locality B-7053-25, Palo-Blanco Mine on the Finca Palo Blanco, about 22 km. northeast of Tapilula (lat. 17°1'N, long. 92°2'W), acc. no. 2072. Nymph fragments (paratype), head, pronotum, and legs from locality B-8416-3, Copainala, north and west of Tuxtla Gutiérrez (lat. 17°1'N, long. 93°1'W) from West Chiapas, acc. no. 2063. Nymph fragments (paratype), part of head and legs, from locality B-8413-126, Ixhuatan, on Rio Tapilula (=Rio Teapa) (lat. 17°1'N, long. 93°1'W), acc. no. 2063. Nymph fragments (paratype), head, antenna, pronotum, and legs, in two pieces of amber from localities B-8414-6 and B-8414-7, Chicoasen (=Chicoacen), lower end of right bank of Grijalva River canyon, acc. no. 2063. Nymph fragments (paratype), part of head and antenna, from locality B-7051-9, Vega de la Campana on Rio San Pedro, 7 km. north of Simojovel (lat. 17°1'N, long. 92°2'W), acc. no. 2072. Nymph fragments (paratypes), head, pronotum, legs, and part of abdomen in three pieces of amber, from localities B-7049-6, B-7049-7, and B-7049-8, southeast of Bachajon, upper end of the Rio de la Virgin (lat. 17°1'N, long. 92°1'W), acc. no. 2072. Nymph fragments (paratype), front leg, from locality B-7045-59, big landslide between Santa Catarina and Portugal, acc. no. 2072.

The holotype soldier and paratypes—imagoes and nymphs—are deposited in the Museum of Paleontology, University of California, Berkeley, California.

ETYMOLOGY: The name *electromexicus* means fossil amber from Mexico (electro < Greek ēlektron, "amber").

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